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Microarthropods

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I. Introduction

This chapter is concerned mainly with the feeding habits of Collembola, or springtails (apterygote, "primitive" insects, with basically mandibulate mouthparts), and of Acari, or mites, which have basically chelate jaws known as chelicerae. These are usually the most abundant animals in dry-funnel extracts of plant litter, and the term microarthropods is often used in terrestrial studies to refer to these two groups together. Other groups which may also be encompassed within this term include Diplura, Thysanura and Protura (apterygotes), Symphyla and Pauropoda (small myriapods), and Tardigrada ("degenerate" arthropods).

Many species of microarthropod are zoophagous, while certain phytophages consume living tissues of higher plants. We shall deal with the

utilization of higher-plant litter and lower plants, which are the major food sources of phytophagous litter-dwelling species. Particularly with lower plants, it is often difficult to distinguish between the ingestion of living and of dead tissues (e.g. in gut contents), so that some of the examples in this chapter may not be true litter feeders.

Most Collembola crush their food between mandibular plates, although some possess styliform, piercing and sucking mouthparts. Styliform chelicerae occur in various families of the acarine order Prostigmata, but in

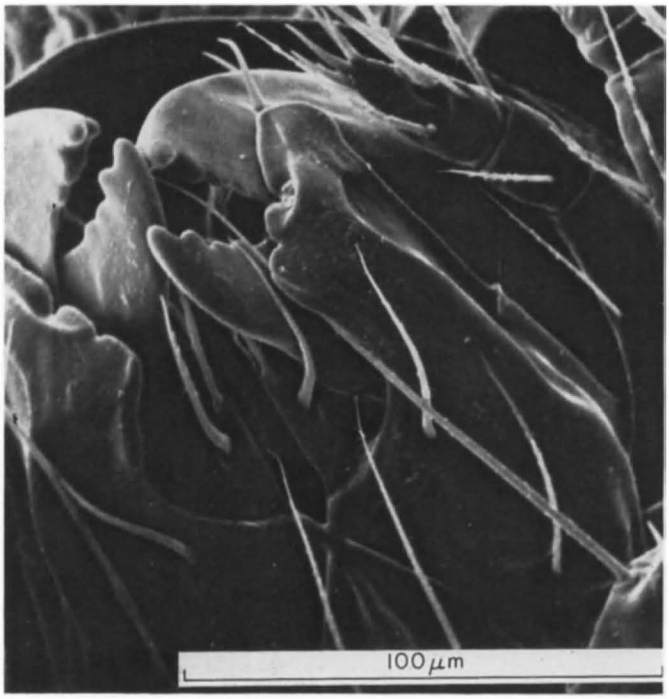


Fig. 1. Mouthparts of a phthiracaroid mite, with chelate-dentate chelicerae. (Reproduced by permission of the Trustees of the British Museum (Natural History).)

many of these cases it is not known whether the food consists of animal or of plant tissues. Most litter-dwelling Astigmata and the vast majority of Cryptostigmata, or oribatids, have chelate-dentate chelicerae (Fig. 1) and are phytophagous, as are certain species of the predominantly zoophagous order Mesostigmata, notably among the suborder Uropodina. In most sites Acari are more abundant than Collembola, with Cryptostigmata (or, occasionally, Prostigmata) numerically dominant among the mites.

The ecology of microarthropods in litter and soil has been discussed

by Kühnelt (1961) and Kevan (1962) and, more recently, by Wallwork (1970), while quantitative methods in soil ecology are considered by Phillipson (1971). Review articles include those by Christiansen (1964) and Hale (1967) on Collembola, Wallwork (1967) on Acari, Edwards *et al.* (1970) on invertebrates, and Butcher *et al.* (1971) on Collembola and Acari. In an important paper by Schuster (1956), plant-feeding oribatid species were classified as *macrophytophagous* (generally feeding solely on higher-plant remains, the gut contents including at most only insignificant amounts of, for example, fungal fragments) or *microphytophagous* (with gut contents consisting entirely of lower-plant remains, with only occasional traces of phanerogam material) or *unspecialized* (gut contents either include a mixture of cryptogam and phanerogam remains, or are mainly of one type in some individuals and of a different type in others of the same species). Luxton (1972), in his review of oribatid nutritional biology, uses the term *panphytophagous* instead of unspecialized.

II. Types of Food and Feeding Habits

A. Cryptogams

Despite numerous population and community studies of microarthropods associated with cryptogams (see Frankland, Chapter 1), there is relatively little information on their feeding habits. For example, mosses and lichens have long been recognized as likely habitats for high population densities of animals such as tardigrades, mites and Collembola, while oribatids are commonly known as moss mites (Jacot, 1930) or Moosmilben (Willmann, 1931), but Gerson (1969) points out that the exact nature of the relationships between oribatids and mosses is largely unknown.

1. Fungi

Acari and Collembola are frequently found in the sporophores of polypores (Graves, 1960; Pielou and Matthewman, 1966), and some of these inhabitants are thought to be mycophagous (Graves, 1960). Hingley (1971) concluded from gut-content studies that ten species of microarthropod, including *Thyreophagus* sp. (Astigmata), *Cepheus latus* C.L.K. (Cryptostigmata) and *Isostoma arborea* (L.) (Collembola), were feeding predominantly on remains of dead stromata of the ascomycete *Daldinia concentrica*.

Most studies of mycophagy among litter microarthropods have involved the microfungi on plant debris. Ever since Michael (1884) found that mouldy cheese provided a satisfactory diet for various oribatids, numerous microarthropod species have been cultured either on fungi or on organic matter undergoing fungal decay (Woodring, 1963; Butcher *et al.*, 1971). Observations of feeding in culture, coupled with the dominance of fungal

remains in the visible gut contents of certain species, led many to conclude that fungi were among the most important components of the food of many Acari and Collembola (Forsslund, 1939; Macnamara, 1924). More extensive surveys of gut contents and the offer of a wider range of foods have shown that some species are indeed strictly mycophagous, but that others also feed on other cryptogams or are panphytophagous. Further details of mycophagy will be found in section IIB.

2. Lichens

Lichens were noted by Michael (1884) as a favourite resort of oribatids, and several species have been cultured on lichens, including *Camisia segnis* (Hermann), *Platynothrus peltifer* (C.L.K.) and *Nothrus* spp. (Grandjean, 1950), *Scheloribates laevigatus* (C.L.K.) and *Oppia nova* (Oudemans) (Woodring and Cook, 1962). Two oribatid species of the genera *Scapheremaeus* and *Cryptoribatula* which dwell in and feed on crustose lichens were described by Jacot (1934). In his studies of saxicolous and arboreal oribatids Travé (1963, 1969) described certain species, such as *C. segnis* and *Pirnodus detectidens* Grandjean, as strictly lichenophagous, and also recorded the presence of Collembola, Thysanura and Prostigmata in lichens. The oribatid *Maudheimia petronia* Wallwork forms feeding cavities in *Usnea antarctica* (Gressitt and Shoup, 1967), while *Halozetes belgicae* (Mich.) probably feeds on foliose lichens (Strong, 1967). Schuster (1956) recorded fragments, apparently of lichens, in the gut contents of most microphytophagous and "unspecialized" oribatids which he examined.

3. Algae

Certain microarthropods of littoral and salt-marsh sites are directly or indirectly dependent on algae for food. Mites in the intertidal zone and those associated with early stages of *Fucus* (wrack) decomposition are mainly predatory, but intertidal species of *Ameronothrus* (Cryptostigmata) are algivorous (Evans *et al.*, 1961). Oribatids and Astigmata on wrack in the later stages of decay are probably largely mycophagous (Schuster, 1966), and although Moeller (1967) concluded that Collembola have no visible effect on wrack decomposition, Zachariae (in the discussion of Moeller's paper) suggested the likely importance of fungi to these wrack inhabitants. *Hygroribates schneideri* (Ouds.) is an example of an algivorous oribatid from salt marshes which may also ingest fungi (Luxton, 1966).

Lund (1967) points out that scarcely any study has been made of grazing on soil algae, and the same applies to most terrestrial habitats. Limited experiments with antarctic microarthropods suggest that algae may be an important food source for certain species such as the collembolan *Cryptopygus caecus* Wahlgren (Tilbrook, 1967) and the prostigmatid *Nanorchestes*

antarcticus Strandtmann (Gressitt and Shoup, 1967). Various microarthropods have been successfully cultured on *Protococcus* or *Pleurococcus* including Collembola (Healey, 1971), the oribatids *Nanhermannia nana* (Nicolet), *P. peltifer*, *Nothrus silvestris* Nicolet, *Camisia* spp., *Damaeus* spp. and immatures of *Galumna* spp. (Woodring, 1963; Littlewood, 1969). Tarman (1968) observed that *Pleurococcus* cells were broken open by the chelicerae of oribatids, while Schuster (1956) and Tarras-Wahlberg (1961) recorded that oribatids such as *Xenillus tegeocranus* (Hermann) and *Nothrus pratensis* Sellnick prefer these algae to phanerogam litter. Epiphytic algae on bark are often plentiful in forest and heathland litter, but there is very little evidence of the importance of these or of soil algae as food for microarthropods. Algal remains were detected among the gut contents of 14 oribatid species, including *X. tegeocranus* and *Belba* spp., by Schuster (1956) and also in *P. peltifer* and the Collembola *Folsomia quadrioculata* (Tullberg) and *Onychiurus quadriocellatus* Gisin (H. Faasch, personal communication).

4. Bryophytes

Very high microarthropod densities are indicated by seasonal means of *ca.* 28 cm^{-2} for Acari plus Collembola under mosses on limestone boulders (Wood, 1967), and by a mean of 27·5 cm^{-2} of moss for the collembolan *Cryptopygus antarcticus* Willem, which is the dominant arthropod of maritime Antarctica (Tilbrook, 1967). Gerson (1969) commented that arthropods could find shelter, as well as food, among mosses, and Strong (1967) suggested that microclimatic requirements of large species such as *C. antarcticus* might be more significant than the food value of the mosses. Nevertheless, various oribatids, such as adults of *Galumna nervosa* (Berlese) (Sengbusch, 1954), and Collembola, including *Isotoma klovstadi* Carpenter (Pryor, 1962), have been cultured on mosses, while certain tardigrades (Kühnelt, 1961) and Prostigmata (Gerson, 1972) are known to feed on living mosses.

Identifiable remains of moss tissues, among other plant material in gut contents, were recorded in four species of oribatid (including *Liacarus* sp.) out of 40 examined by Schuster (1956), and in *Tomocerus* spp. (Collembola) by McMillan and Healey (1971). The occurrence of faecal pellets of isotomids beneath *Polytrichum* led Drift (1964) to conclude that these Collembola were the only mesofauna of importance in the breakdown of this moss in an inland dune site.

5. Pteridophytes

Elton (1966) found a flourishing fauna, including microarthropods, in *Pteridium* (bracken) litter, and further evidence from *Pteridium*-dominated

sites is provided by maximum densities of 50,000 m^{-2} for the oribatid *P. peltifer* (Harding, 1973), and of 13,100 m^{-2} for *Onychiurus procampatus* Gisin, a species which comprised *ca.* 70% of the collembolan population biomass in Healey's (1967) site. Healey (1967) conducted quantitative feeding experiments with this species on fungi which decompose *Pteridium* (Frankland, Chapter 1), while preliminary, unpublished tests by the present authors indicate that a range of oribatid species will not feed on *Dryopteris* prothalli, but much remains to be investigated concerning the role of microarthropods in the decomposition of litter of pteridophytes and other cryptogams.

B. Trees, Shrubs and Other Phanerogams

1. Laboratory Evidence

Most microarthropods cannot ingest freshly fallen leaves of trees, particularly if this litter is dry. Among Collembola, Schaller (1950) recorded high mortalities in five out of seven species cultured on fresh litter of various trees, ranging from *Alnus glutinosa* (alder) to *Quercus pedunculata* (oak), while Dunger (1956) observed traces of feeding by *Folsomia fimetaria* (Tullberg) on fresh litter of only *Alnus* and *Sambucus nigra* (elder). Hartenstein (1962*a*) found no evidence of feeding on fresh litter by any of 20 species of Cryptostigmata, but, according to Riha (1951), *Pelops* sp. prefers to feed on litter which is dry, rather than partially decomposed, and *Achipteria* sp. possibly shows a similar preference for the epidermis of dry *Tsuga canadensis* (hemlock) needles (Wallwork, 1967). Kühnelt (1961) commented that machilids (Thysanura), when abundant, may be of significance among the initiators of decomposition, feeding, for example, on fresh *Fagus* litter.

There is virtually no information on the longevity or fecundity of those species that can feed on fresh litter, but most litter-feeders seem to prefer to utilize moist, partially decomposed leaves (Kühnelt, 1961). Phthiracaroids, for example ("box mites" or "armadillo mites"; Cryptostigmata), feed readily in culture on fresh *Quercus* leaves which have been immersed in water for as little as two days (Harding, 1966), but sustained culturing of microarthropods usually necessitates providing material which is somewhat more decomposed. Attack normally starts on the abaxial surface of the leaf, where oribatids tend to remove the superficial, non-lignified tissues of the midrib and main veins, before proceeding to feed on intervein tissues (Schuster, 1956; Führer, 1961). Removal of the lower epidermis and mesophyll from the regions between the finest veins produces a pattern which is common to several groups of animals, particularly when feeding on leaves of *Quercus* and *Fagus*. This "Fensterfrass" (Schaller, 1962) was

described by Noordam and Vlieger (1943) as the "normal mastication pattern" of Collembola such as *Onychiurus armatus* and *Tomocerus minor* (Lubbock), and of various oribatids (e.g. *Hermannia gibba* (C.L.K.), *N. silvestris* and *P. peltifer*) on *Quercus*. Complete perforation of intervein regions, resulting in "Lochfrass" (Brauns, 1954) or "Skelettfrass" (Dunger, 1964) can be effected by Collembola on leaves of *Sambucus*, *Alnus* or *Carpinus betulus* (hornbeam) (Schaller, 1950; Dunger, 1956), but similar patterns on *Quercus* or *Fagus* are usually associated with more robust animals such as oribatids of the genus *Liacarus* (Schuster, 1956) or of the superfamily Phthiracaroidea; the latter may also consume some of the finer veins, forming circular feeding areas (Riha, 1951; Murphy, 1953).

Feeding within petioles and midribs of broad-leaved species has been recorded mainly among immature oribatids, especially phthiracaroids, e.g. *Steganacarus diaphanum* Jacot in *Fagus grandifolia* petioles (Hartenstein, 1962*e*) and *Steganacarus* sp. and *Phthiracarus anonymum* Grandjean in *Quercus* and *Fagus* (Harding, unpublished). Endophagous development of *Adoristes ovatus* (C.L.K.) and of *Steganacarus* and *Phthiracarus* spp. in conifer needles was described by Jacot (1936, 1939; see also Murphy, 1953; Hartenstein, 1962*e*); eggs were laid on needles which had been partially decomposed by fungi, and the immature stages fed within, chewing an exit hole when mature. Adult phthiracaroids in culture have been seen to consume all but the vascular tissues of needles (Murphy, 1953; Führer, 1961; Hartenstein, 1962*e*), but attacks by sminthurid Collembola are largely ectophagous (Zachariae, 1963).

Among the few published observations of oribatids feeding in culture on stems and roots are Michael's (1884) record of burrowing by *Minunthozetes semirufus* (C.L.K.) in grass stems, feeding on *Calluna vulgaris* stems by *Steganacarus magnus* (Nicolet) (Webb and Elmes, 1972), and the preference of *Rostrozetes flavus* Woodring for the decomposing outer tissues of roots (Woodring, 1965). Among Collembola, Schaller (1950) described feeding by *O. armatus* within roots, while Kooistra (1964) found that *F. quadrioculata* showed a preference for decaying roots of *Trifolium repens*.

2. *Field Evidence*

(*a*) *Leaves*. Noordam and Vlieger (1943) attributed normal mastication patterns (see above) on litter in a *Quercus* site to feeding by microarthropods. However, Zachariae (1963, 1965) concluded that these patterns could also be produced by other animals or by physical processes, and that microarthropods were relatively unimportant in comminuting *Quercus* or *Fagus* litter; Collembola and non-predatory mites, and possibly also pauropods, symphylids and proturans, were thought to be feeding on the microflora, or, at most, on decomposed litter fragments, including macroarthropod

pellets. Sminthurids and certain oribatids ingested less decomposed leaves, but they were considered to play a subsidiary role to macroarthropods and lumbricids in Zachariae's sites. Where damp *Fagus* leaves accumulated in places inaccessible to larger animals, e.g. under logs and stones, ideal conditions were provided for the development of leaf-feeding phthiracaroids. On the basis of performance in culture, microarthropods should be able to feed more readily on leaves with a higher nitrogen content than *Quercus*

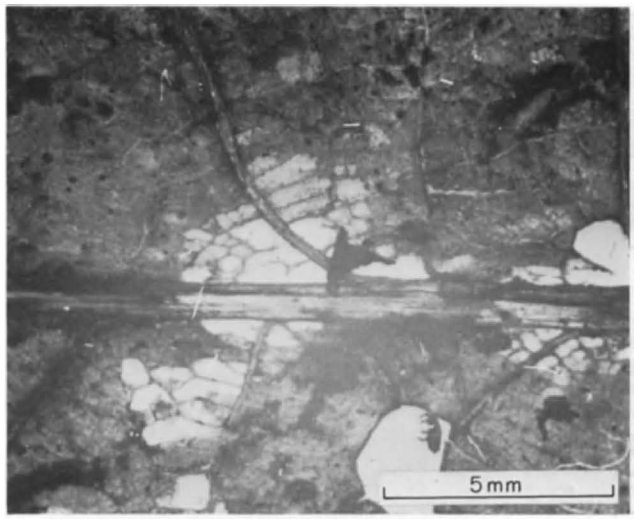


Fig. 2. Part of a *Quercus* leaf from the forest floor, showing stripped midrib and veins, Fensterfrass and Lochfrass, and an adult *Platynothrus peltifer*. (Photograph by P. W. Murphy.)

or *Fagus*, but Zachariae considered that these richer food sources were normally almost monopolized by the macrofauna.

In a mull-like moder site under *Quercus*, *Fagus* and *Sambucus*, where lumbricids were virtually absent and molluscs and macroarthropods scarce, Harding (1966) observed exploitation of *Sambucus* remains by scatopsid larvae (Diptera), but there were also numerous examples of leaflets being perforated by adults and immatures of *Platynothrus peltifer*. *Fagus* and *Quercus* leaves exhibited stripped midribs and veins, Fensterfrass and fine perforations of the lamina; this damage was often accompanied by faecal pellets similar to those of oribatids in culture, and occasionally adults of *Phthiracarus nitens* (Nicolet), *Rhysotritia duplicata* (Grandjean) and *P. peltifer* were found on the damaged areas (Fig. 2). Microphytophagous mites such as *Galumna lanceata* (Oudemans) (Fig. 3) and *Ceratoppia bipilis* Hermann were sometimes seen on newly fallen *Quercus* litter,

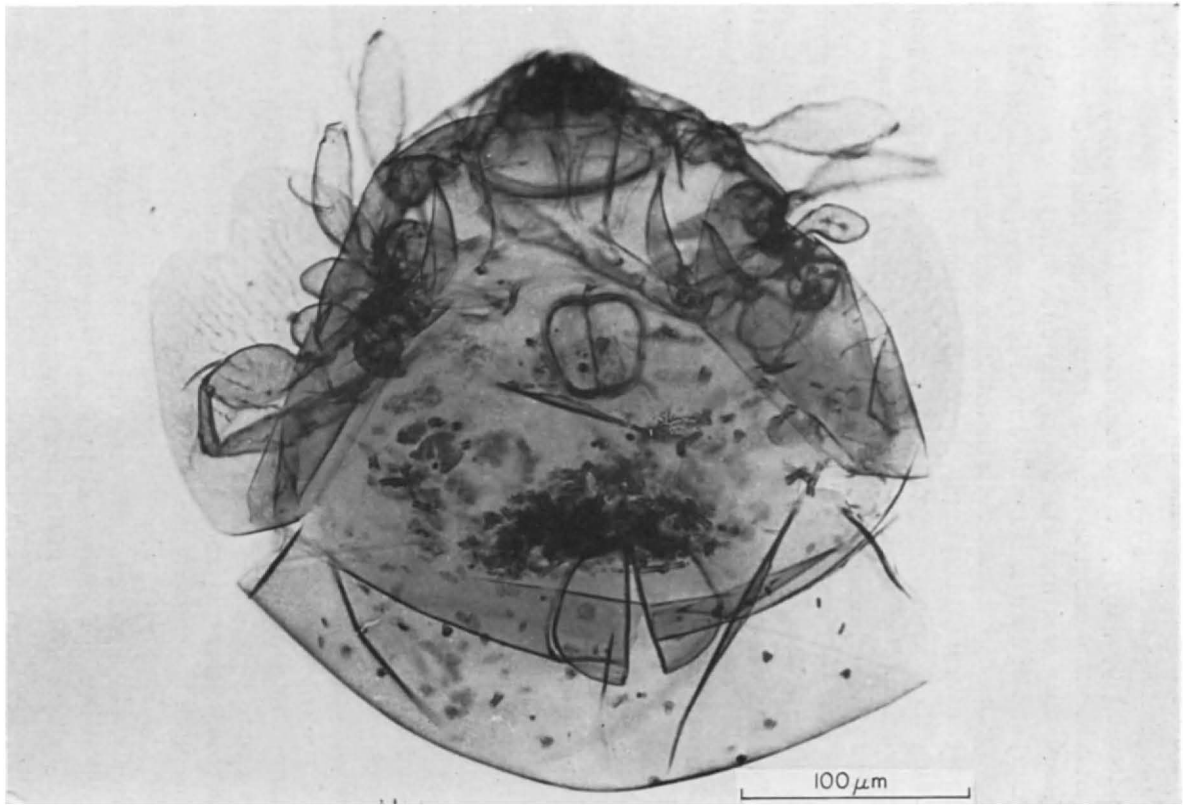


Fig. 3. *Galumna lanceata* adult, with fungal gut contents. (Photograph by P. W. Murphy.)

whereas the most abundant oribatid, *Tectocepheus velatus* (Mich.), occurred mainly among fine detritus in the A_F sub-horizon, and anoetids (Astigmata) moved in moisture films on debris, presumably filter-feeding on micro-organisms (see Hughes, 1953).

Anderson (1970, 1971; see also Anderson and Healey, 1970) examined the gut contents of oribatids removed from gelatine-embedded sections of the forest floor of a mor-like moder site under *Castanea sativa* (sweet chestnut) and of a *Fagus* site with a mull-like moder, and discerned that certain species had characteristic distributions and feeding habits. *Carabodes labyrinthicus* (Mich.) in the upper sub-horizons fed mainly on fungi, including those associated with freshly fallen litter and with humified material transported by lumbricids. The panphytophage *Hermanniella granulata* (Nicolet) ranged between the A_0 and A_{F2}, feeding primarily on *Castanea* leaves in various stages of decomposition, but also on lower plants. Most adults of *Steganacarus magnus* inhabited the A_{F1}, feeding mainly on relatively undecomposed mesophyll. The characteristic species of the A_{F2} was *Rhysotritia ardua* (C.L.K.), which as adults fed on raw humus and mycorrhizal fungi; a few were also found in deep pockets of *Fagus* litter in the A_{00}, resembling the situation described by Zachariae (1965; see p. 532). Collembola were not preserved well in these sections, so specimens of three species were collected from the *Castanea* site, their gut contents dispersed on gridded Millipore filters, and an assessment made of the relative abundance of various types and sizes of particles (Anderson and Healey, 1972; see also McMillan and Healey, 1971). The proportion of individuals with empty guts, presumably associated with moulting, ranged among the species from 38 to 54%. The relative amounts of leaf and fungal material varied seasonally, but on average over 90% of the particles in *Orchesella flavescens* (Bourlet) were of higher plant origin, signifying feeding on superficial, relatively undecomposed litter, whereas a fungal content of *ca.* 40% in *Tomocerus* spp. suggested that the diet of deeper dwelling species consisted largely of partially humified leaf material (Figs 4 and 5).

Bal (1968) compared laboratory feeding patterns with evidence of faunal activity in thin sections of the humus profile in two adjacent moder sites. Under *Quercus rubra*, microbially conditioned leaves in the A_F were skeletonized by mycetophilid larvae (Diptera) and by *Nothrus silvestris*, the oribatid pellets containing cell walls and hyphae, while midribs were mined by *Rhysotritia minima* (Berlese). Endophagous activity was also evident in *Pseudotsuga taxifolia* needles, mainly by all stages of *Rhysotritia* spp. and *Steganacarus striculus* (C.L.K.) in the A_{F2}.

Sectioning of *Pinus sylvestris* needles from a mor site (Kendrick and Burges, 1962) revealed that the formation of pellet-filled cavities in the

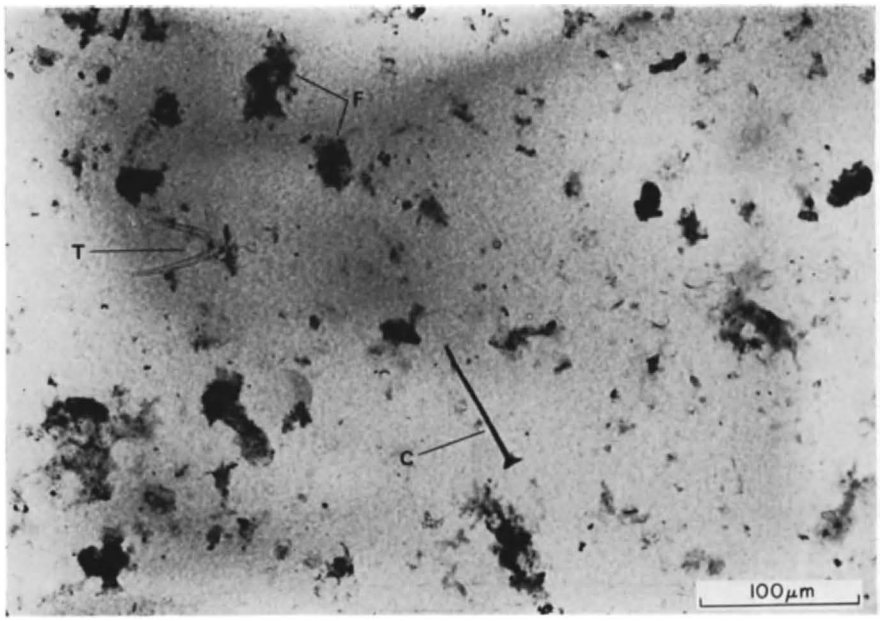


Fig. 4. Gut contents of *Orchesella flavescens*, including leaf fragments (F), trichome (T) and conidiophore (C). (Reproduced with permission from Anderson and Healey, 1972.)

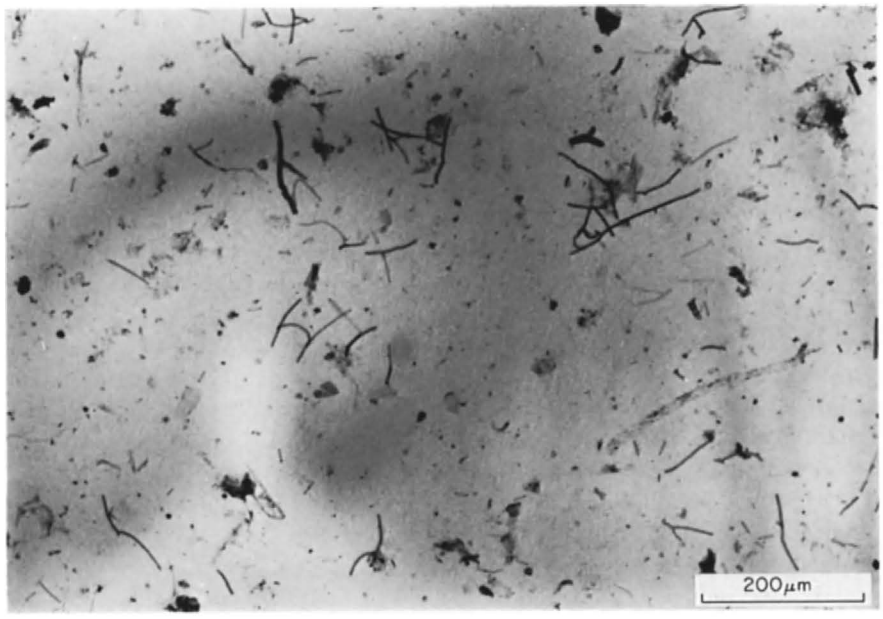


Fig. 5. Gut contents of *Tomocerus minor*.
(Reproduced with permission from Anderson and Healey, 1972.)

mesophyll of needles in the A_{F1} was apparently dependent on a preliminary, internal attack by fungi. From the species list for this site, which does not include phthiracaroids, it seems likely that these cavities were produced by *Adoristes ovatus*, an oribatid recorded by Jacot (1939) as developing within conifer needles (see p. 495) and by Michael (1884) from needles of *Ulex* (furze). Faecal evidence suggested that mites and Collembola fed on hyphae and conidiophores on the needle surface.

Truly ectophagous behaviour by Collembola, involving ingestion of needle material, was thought by Zachariae (1963) to be of minimal importance, except when sminthurids were locally abundant. Seasonal variations in the gut-content composition of Collembola in a *Pseudotsuga* site were described by Poole (1959), who concluded that in general larger species such as *Tomocerus longicornis* (Muller) were feeding mainly on fungi, with decaying mesophyll as an alternative, while smaller species (e.g. *Tullbergia krausbaueri* Borner) possibly subsisted on humus fragments or arthropod pellets.

Animals responsible for the breakdown of plant material in particular sites may also be studied by using radioactively labelled material. For example, Gifford (1967) recorded relatively high levels of ^{14}C in oribatids such as *P. peltifer* exposed to tagged *Pinus sylvestris* needles, and Coleman and McGinnis (1970) found that mites belonging to four orders fed on ^{65}Zn-labelled mycelium of *Geotrichum* in field soil, but that Collembola were not labelled, indicating selective feeding in relation to this fungus. Various criteria of ^{137}Cs uptake from *Liriodendron tulipifera* (tulip tree) leaves, including accumulation rate, were employed by McBrayer and Reichle (1971) to distinguish between members of different trophic levels; fungivores included Onychiuridae, Carabodidae and Rhodacaridae (the latter, mesostigmatid family is normally considered predatory), while Isotomidae, Phthiracaridae and Uropodina were classified as litter-ingesting saprophages, and soil-dwelling Symphyla as feeding on translocated organic matter.

(*b*) *Pollen*. Pollen grains make up a large proportion of the diet of certain surface-dwelling Collembola (Christiansen, 1964; Scott and Stojanovich, 1963), as well as being utilized by certain Prostigmata (Evans *et al.*, 1961). Pollen is important to rock dwellers, such as oribatids of the genus *Saxicolestes* (Travé, 1963), but may also be a component of the gut contents of forest-floor Collembola and Acari, including microphytophages (Schuster, 1956; Zachariae, 1965) and panphytophages, such as *Xerillus tegeocranus* (Schuster, 1956); Hammer (1972) found that during the spring certain panphytophagous oribatids fed almost exclusively on *Alnus* pollen.

(*c*) *Fruits and cones*. Microarthropods played a minor role in the decomposition of *Quercus rubra* acorns (Winston, 1956); shell material was

ingested by certain Collembola and oribatids, whereas astigmatids and prostigmatids were mycophagous. Harding (unpublished data) found up to 30 immature phthiracaroids burrowing into the tissues of a single cupule of *Fagus sylvatica*; examination of younger cupules revealed deutova ("eggs") embedded in the surface of the pedicel, the valves and the base

Fig. 6. Phthiracaroid deutovum embedded in valve of *Fagus sylvatica* cupule. (Photograph by R. Turner, Rothamsted Experimental Station.)

of the locule. Larvae burrowed from these sites into the pedicel or valves, developing via nymphs to adults of *Steganacarus* sp. or *Phthiracarus anonymum*, the latter continuing to burrow when adult (Figs 6 and 7). Adults of *Phthiracarus japonicus* Aoki were abundant in *Alnus hirsuta* cones (Aoki, 1967), but although various Collembola were recorded from *Picea excelsa* cones by Arend (1967), the only oribatid was the microphytophage, *Belba gracilipes* Kulcz. In striking contrast, N. R. Webb (personal communication) has obtained up to 50 immatures of *S. magnus* from within a single cone of *Pinus sylvestris*.

(*d*) *Roots*. Living roots may be seriously damaged by certain Symphyla, e.g. *Scutigerella immaculata* (Newport) (Michelbacher, 1938; Edwards, 1961), but in most other cases only dead tissues of roots are ingested by microarthorpods. Thus Führer (1961) demonstrated that *Rhysotritia ardua* preferred to feed on decomposing roots of *Artemisia campestris*. Jacot

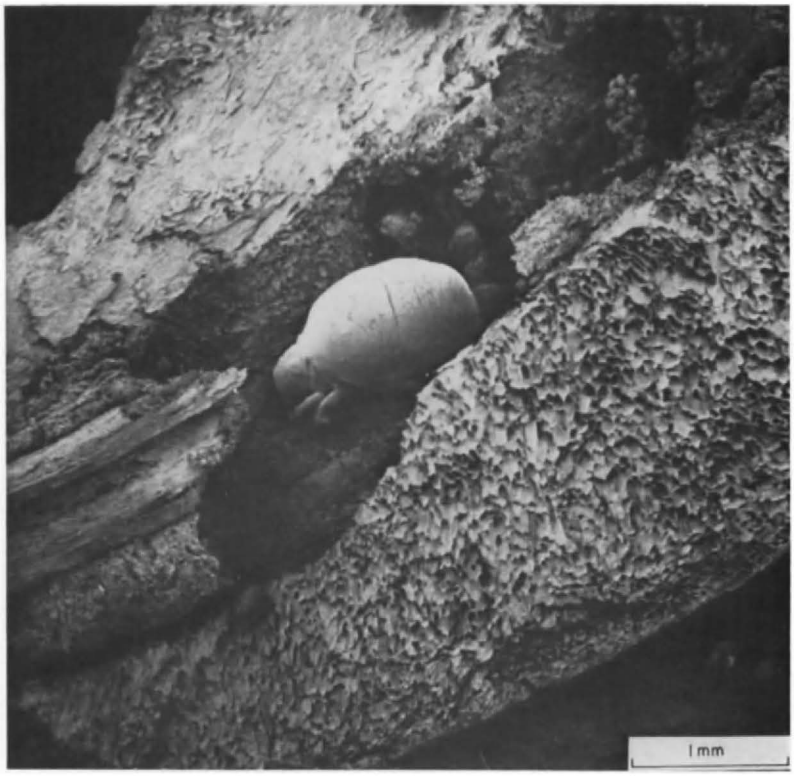


Fig. 7. Phthiracaroid nymph and faecal pellets in burrow within pedicel of *F. sylvatica* cupule. (Photograph by R. Turner, Rothamsted Experimental Station.)

(1936) suspected that *R. ardua* developed inside decaying roots, and this has been confirmed for various species of *Rhysotritia* in sections of tree roots (Drift, 1964; Bal, 1968; Anderson and Healey, 1970). Bal (1968) also found evidence of ectophagous damage to *Quercus* roots by *Nothrus silvestris*. Root-dwelling Collembola are probably mainly mycophagous or ectophagous, e.g. on sloughed cortical material of *Malus* roots (Harding, 1968). The importance of the mesofauna in clearing away dead roots to provide channels for aeration, drainage and the transfer of organic remains was emphasized by Rogers (1939) and Ghilarov (1971).

(*e*) *Wood*. Kühnelt (1961) has summarized the results of authors such as Fourman (1938) and Riha (1951), on the decomposition of tree stumps and fallen branches. The collembolan *Bourletiella hortensis* (Fitch) apparently thrives on undecomposed wood, but normally the main attack commences following decortication, when phthiracaroids and their immatures, Collembola and immatures of *Carabodes labyrinthicus* gain access to the heartwood. Immature mites, including Mesostigmata, phthiracaroids, *Hermanniella granulata*, *Liacarus xylariae* (Schrank) and *Cepheus* were recorded feeding on and in bark. Wallwork (1958, 1967) described the distribution of various xylophagous oribatids (e.g. *Steganacarus diaphanum*) around and within fallen twigs of *Tsuga canadensis* and *Betula lutea*. Burrows of *S. magnus* adults, with side tunnels for immatures, occurred mostly in the heartwood of *Betula* but only in the bark of *Tsuga*, while *Rhysotritia* spp. usually burrowed near the surface of both. *Hermannia* sp. nymphs fed on *Betula* lenticels. Finally, oribatids or their pellets have been recorded in thin sections of fallen twigs. Drift (1964) and Bal (1968)

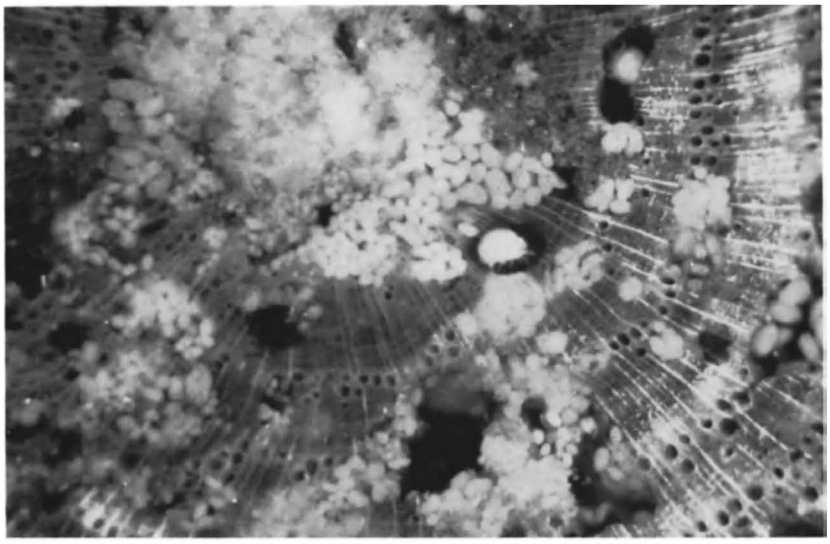


Fig. 8. Section of *Castanea sativa* twig, containing oribatid faecal pellets and *Liacarus xylariae* nymphs. (Reproduced with permission from Anderson, 1970.)

identified pellets of *Rhysotritia* inside *Pinus* and *Quercus* wood, respectively, and Anderson and Healey (1970) and Anderson (1971) found nymphs of phthiracaroids, of *L. xylariae* (Fig. 8) and of *H. granulata* in rotten wood, the latter species often occurring in diplopod tunnels within twigs of *Castanea*.

C. Coprophagy

Vertebrate dung may be colonized by various microarthropods, but most of these, such as macrochelids (Mesostigmata) are predatory.

Feeding on the excreta of litter-ingesting invertebrates is said to be common among Collembola, particularly in small species (Christiansen, 1964), and also among oribatids, mainly as immatures (Wallwork, 1967). However, conclusions based on laboratory experiments should be accepted with caution, and, as Anderson and Healey (1972) pointed out, it is extremely difficult to demonstrate the significance of coprophagy in natural populations of soil animals.

Schuster (1956) recorded that macrophytophagous and unspecialized oribatids fed for several weeks on fresh pellets of isopods, but that pellets obtained from the forest floor were ignored. Collembola such as *Tomocerus flavescens* Tullberg, *F. fimetaria* and *Sinella coeca* (Schött) will comminute the excreta of certain macroarthropods and lumbricids (Schaller, 1950; Dunger, 1956, 1958*a*), but Dunger (1956) found that these species preferred to feed on litter which had not been processed by other animals. On the other hand Wallwork (1958) observed that the oribatids *Galumna formicarius* (Berl.) and *Oppia* spp., found inside fallen *Betula* twigs, could not ingest woody tissue, but they were able to feed on the pellets of endophagous phthiracaroids. According to Wallwork (1967), intraspecific coprophagy is common among immatures of oribatids which are xylophagous as adults, and Rohde (1955) assumed that larvae of *Rhysotritia* sp. in culture were feeding on adults' pellets. However, coprophagy was not observed by Walker (1965) in larvae of *Plesiotritia megale* Walker, where all stages were apparently xylophagous, and is unlikely to occur, at least between adults and larvae, in species where the larvae hatch from embedded deutova (e.g. in beech cupules, see p. 501) and burrow into woody tissues independently of adult feeding activity.

Reports of evidence of coprophagy under field conditions are rare. Nicholson *et al.* (1966) found that pellets of the millipede *Glomeris marginata*, placed on the soil surface in nets, were often visited by Acari, Collembola and enchytraeids and converted into smaller pellets. Bal (1968) reported evidence from soil sections of feeding by *O. quadriocellatus* on pellets of *Quercus*-feeding mycetophilid larvae, but Zachariae (1963) believes that Collembola found among decomposing excreta are microbivorous.

D. Artificial Litter

Harding (1966) used the cellulose-film technique devised by Tribe (1957) to provide microbially conditioned material for cultures of litter-feeding

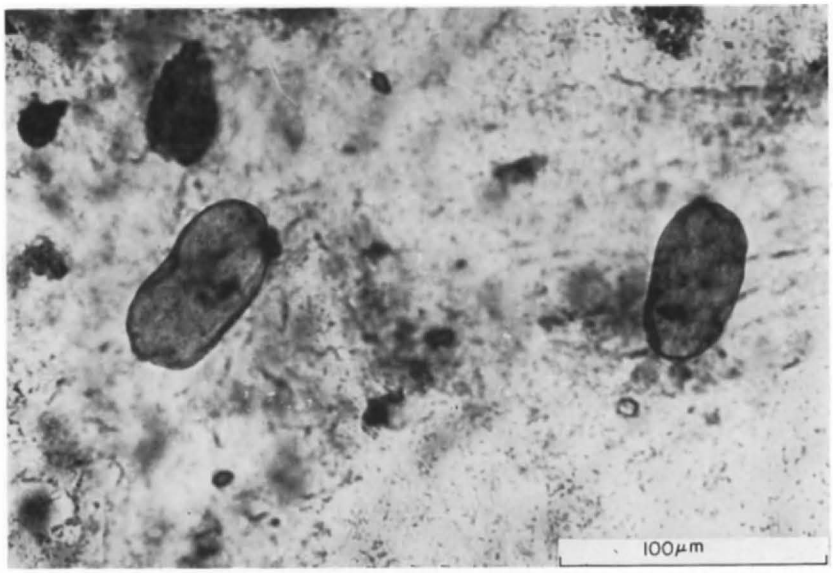
oribatids, including phthiracaroids and the panphytophagous *P. peltifer*, and also for microphytophagous Acari. Evidence of feeding activity in a *Quercus-Fagus* site was obtained by burying cellophane inserts in the forest floor (Harding, 1967). Some of the pellets on these inserts (Figs. 9 and 10) were similar to those of cultured oribatids, including *R. duplicata*, a species observed by Went and de Jong (1966) on cellophane recovered from a forest soil. Small pellets are often difficult to detect in soil sections (Drift, 1964), but very large numbers of pellets of *ca.* 30 μm breadth were produced on inserts in the late summer, possibly by immatures of *T. velatus* and *P. peltifer*.

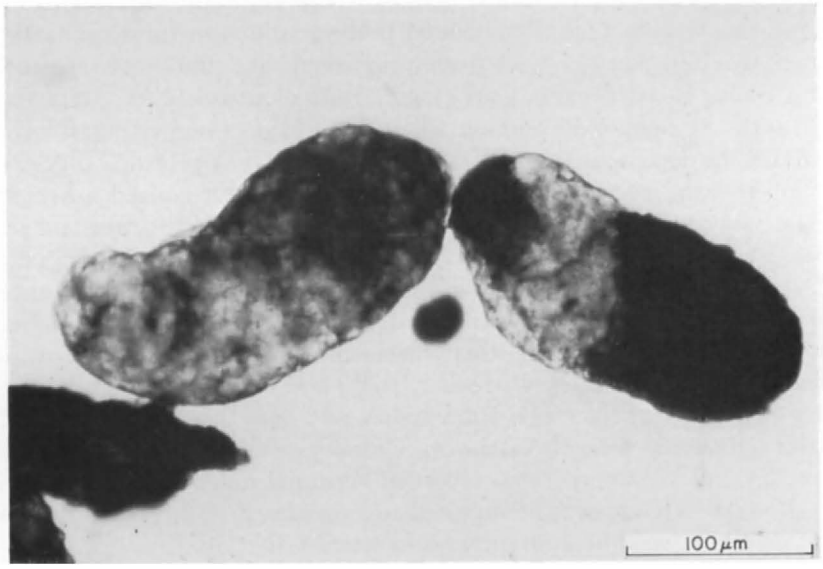
The role of Collembola in the decomposition of filter paper is discussed on p. 509.

E. Successions

Some of the temporal changes in the species composition of populations associated with decomposing litter have been correlated with physical and chemical properties of the litter, e.g. of *Fucus* (Strenzke, 1963). Cernova (1971) suggested that certain microarthropods could be used as indicator species for particular stages in the decomposition of manure. However, Moeller (1965) concluded that variations in the abundance of wrack-dwelling species were largely seasonal, and did not constitute a true, ecological succession. Curry (1969*b*) also distinguished between these two types of temporal variation when discussing faunal changes accompanying the decomposition of grassland herbage. During the decomposition of lucerne and rye straw in soil Naglitsch (1966) recognized a bacterial phase, succeeded by a phase which included Acari (Anoetids and pyemotids), and finally a humification phase, involving Collembola, uropodids, *R. ardua* and other oribatids, pauropods and diplurans. In many papers on succession there are few if any details of the role of the dominant organisms, but it appears that successions of Collembola on wrack (Zachariae, in discussion of Moeller, 1967) and on compost (Gisin, 1952) may be related to microbial successions, and that the animals have little direct effect on litter breakdown. Crossley and Hoglund (1962) and Crossley and Witkamp (1964) recorded an initial invasion of tree litter in mesh bags by a few species of microarthropod, many probably mycophagous, and only later was there an increase in species diversity.

Anderson (1970) found no evidence of a single group of pioneer fauna on *Fagus* or *Castanea* leaves sampled one month after being placed in the forest floor. Insufficient animals were recovered from the litter in mesh bags to ascertain whether there was a faunal succession corresponding to the known microbial succession on these leaf species; Anderson expected the





Figs 9 and 10. Faecal pellets on cellophane inserts recovered from anoak -beech forest floor. (Reproduced with permission from Harding, 1967.)

faunal species composition to change as microhabitats and exploitable substrates, including micro-organisms and their exometabolites, increased in diversity, but more data are needed to support this hypothesis.

F. Preference and Feeding Specificity

Food preference may be assessed in various ways: by measuring ingestion or defaecation rates on a range of foods when offered in combination ("choice" experiments) or separately; by noting which foods are consumed before others; or by determining which food has the most animals associated with it. The precise relationships between these various criteria are in many cases unknown (Hayes, 1963).

Dunger (1956) found that if certain species of trees and shrubs were arranged in series according to the volume of litter ingested by *F. fimetaria*, then this series agreed closely with that of Wittich (1943) for natural decomposition rates, ranging from *Sambucus* to *Fagus*. Berthet (1964) observed that *N. palustris* fed on *Carpinus* leaves, but not on *Corylus avellana* (hazel), *Fagus* or *Quercus*, whereas *S. magnus* fed on each species in turn, starting with *Carpinus*, on which ingestion rates were considerably higher than for *Quercus* or *Fagus* (see p. 513). Schuster (1956) and Hayes (1963) were unable to detect preferences among oribatids for particular litter species, but Hayes observed larger numbers of phthiracaroids and their pellets on conifer needles in later stages of decay, and Führer (1961) recorded that *R. ardua* adults were about 20 times more abundant around dead roots of *Artemisia campestris* than around healthy ones. H. Faasch (personal communication) observed feeding by *P. peltifer* on shade leaves of *Fagus*, but virtually none on sun leaves (*cf.* Heath and Arnold, 1966).

It is rarely possible to determine defaecation rates on different foods from data published on preference experiments, but by culturing oribatids such as *R. duplicata* on each of the foods which were simultaneously being used in choice experiments, Harding (1966) found that in most cases there were appreciably higher rates of pellet production on those litter species or stages of decomposition (of litter or cellophane) which attracted most mites, and that pellets were significantly larger, as well as more abundant, on more decomposed cellophane.

Hartenstein (1962*a*) gives several examples of preference for particular species of fungi among strictly fungivorous oribatids, e.g. *Trichoderma koningi* by belbids; *Aspergillus niger* repelled all species except *Oppia nova*. The behaviour of various Collembola and Acari (including oribatids, Mesostigmata and Astigmata) when offered *Trichoderma viride* or *Rhizopus nigricans* was investigated by Farahat (1966), who found that certain species in all groups ingested hyphae and spores, whereas *Achipteria*

coleoptrata (L.) fed only on hyphae, and *Oppia nitens* C.L.K. only on spores. Other species of *Oppia*, sminthurids and phthiracaroids failed to feed at all, and populations declined in soils containing these fungi. Singh (1969) presented gut-content microflora to Collembola, and observed slightly different preferences between *T. longicornis* and *O. armatus*, both of which fed on hyphae and spores, whereas only spores were seen in *Neanura muscorum* (Templeton). Mignolet (1971) concluded that fungi cultured from faeces could be used to demonstrate feeding specificity in the microphytophagous *Damaeus onustus* C.L.K., but not in the panphytophagous *Euzetes globulus* Nicolet, nor in the macrophytophagous *Nothrus palustris* C.L.K., the latter failing to feed on any of the fungi. Preference experiments with *Nothrus biciliatus* C.L.K. led Saichuae *et al.* (1972) to the conclusion that the suitability of particular fungi as food may alter as these age, possibly due to production of toxins, and that pellet production may be an unreliable parameter for suitability, since some fungi were consumed but failed to support development of immatures. Luxton (1972) has recorded relative amounts of feeding by various oribatids from a *Fagus* woodland when offered a wide range of fungi, yeasts and bacteria from the same site. Two species of *Steganacarus* consumed none of this microbial food, whereas *Phoma* sp. was selected by *Adoristes ovatus* and by adults of *Damaeus clavipes* (Hermann), immatures of the latter preferring *Trichoderma viride*. *Belba corynopus* (Hermann) was the only species which preferred *Penicillium*, while *Gustavia microcephala* (Nicolet) specialized on bacteria, and *Hypochthonius rufulus* C.L.K. included bacteria among a wide range of foods.

Dunger (1962) concluded that the preference order for various species of tree litter was remarkably similar in members of different faunal groups, e.g. Diplopoda and Collembola. Earlier (Dunger, 1958*b*), possible factors had been suggested as being responsible for food selection by macrofauna, and these were also discussed, with reference to *Lumbricus terrestris*, by Satchell and Lowe (1967), who confirmed Dunger's view that texture is of little significance in determining palatability, but that the latter is broadly correlated with nitrogen and soluble carbohydrate levels; the increased palatability which often accompanies weathering was thought to be due partially to microbial degradation of various distasteful substances, such as tannins (see Williams and Gray, Chapter 19). Heath and Arnold (1966) considered that palatability of litter was more important than digestibility in determining the preferences of soil fauna. The preference of many litter-feeding microarthropods for decaying vegetation, sometimes at a particular stage, also suggests the importance of micro-organisms, but these could be providing food, either in the form of microbial tissues or as litter breakdown products (exometabolites), rather than merely decomposing tannins.

The presence of living micro-organisms is apparently essential for the feeding of certain species. Woodring and Cook (1962) showed that larvae of the oribatid *Ceratozetes cisalpinus* Woodring and Cook, derived from surface-sterilized eggs, were unable to consume aseptic lichen until they had ingested fungal hyphae. Decayed leaves, which are the preferred food of *Protoribates lophotrichus* Berlese, were rendered unpalatable by heating, sulphanilamide treatment or prolonged use in culture (Hartenstein, 1962*d*); this suggested that living micro-organisms were important, either multiplying in the gut and being digested or aiding digestion as gut symbionts. Various bacteria and other bodies have been demonstrated in the gut of this and other oribatid species, e.g. by Woodring (1963) in *Galumna* adults, by Rohde (1955) in *Rhysotritia*, and by N. Haarløv (personal communication) in the proventricular caeca of *P. peltifer*, but it is not known whether these are symbiotic. Finally, Törne (1967, 1968) has stressed the importance of extraintestinal cellulolytic attack in Collembola associated with decomposing filter paper; interspecific variation in the ability to utilize this substrate is probably a consequence of characteristic gut floras, the microbes being spread mainly via the faeces.

Luxton (1972) concedes that microbes may be essential in the diet of *Protoribates* and other panphytophages, but suggests that they are not utilized in macrophytophages, since he was unable to demonstrate in *Steganacarus* spp. the presence of enzymes capable of attacking trehalose, an important reserve carbohydrate in certain fungi. Fungal remains are said by Luxton to be rare in the gut contents of macrophytophages (but see p. 510), and he suggests that the greater rates of pellet production on later stages of litter decomposition, e.g. by phthiracaroids on conifer needles, are a consequence of reduced availability of nutrients in litter tissue, due to microbial activity. It seems to us, however, that microbial protoplasm or exometabolites could be utilized by these macrophytophages, thus explaining the fact that these mites prefer to feed on microbially conditioned foods, when offered a choice, congregating there as well as producing pellets at a greater rate. Attraction by living bacteria or their metabolic products was demonstrated by Führer (1961) using an arrangement of tissue extracts from *Artemisia* roots which precluded actual feeding by *R. ardua*. If these microbes are not actually providing nourishment, and if texture is unimportant in determining palatability, then the only remaining way in which they could be indispensable is in enabling the animals to recognize the plant material as food; this was one possible suggestion made by Littlewood (1969) to account for the cessation of feeding by surface-sterilized microphytophagous and panphytophagous oribatids on aseptic algae, a diet which is unlikely to require symbiotic assistance except, perhaps, to deal with mucilage.

It is unwise to consider the results of a choice experiment as representing an immutable order of preference of a particular species, since choice may vary with time and pre-test conditions (Drift, 1965). Healey is quoted by Hale (1967) as suggesting that the results of preference tests with Collembola such as *O. procampatus* are of little significance, because of the limited sensory powers of these species, but Coleman and Macfadyen (1966) found greatest numbers of *O. procampatus* recolonizing irradiated soil cores containing species of fungi which Macfadyen (1969*b*) described as being selected in the laboratory. If individuals in nature are able to exercise some choice over food, then there are indications of more rapid development on certain foods, e.g. *Belba kingi* Hartenstein on *Trichoderma koningi* (Hartenstein, 1962*b*).

Certain species, such as those found in particular kinds of lichen, are possibly as fastidious in their natural feeding as they appear to be in culture. The difficulties which are encountered in trying to rear certain oribatids in culture suggest that the immatures of these species are more food-specific than the adults (Arlian and Woolley, 1970). Nevertheless, studies of feeding habits, particularly those based on examination of gut contents of animals collected from different sites or at different seasons, generally indicate that a given species ingests a variety of foods. Schuster (1956) recorded a predominance of fungal remains, with some algal and lichen fragments, in the microphytophagous *Damaeus auritus* (C.L.K.), whereas panphytophages such as *Liacarus* and *Notaspis* spp. contained a wider range of dietary components. Many Collembola are panphytophagous (Dunger, 1956), but the potential choice as indicated in culture may be restricted in the field by availability (Wallwork, 1970), so that the gut-content composition of a particular species may vary markedly, either between sites (Gilmore and Raffensperger, 1970), or, within one site, at one time or seasonally (Poole, 1959; Anderson and Healey, 1972); intraspecific variation between sites may be more marked than interspecific differences within one site (Anderson and Healey, 1972). Schuster (1956) was unable to discern seasonal variation of this kind in oribatids, but Anderson (personal communication) found considerable intraspecific variation, both within and between samples of oribatids from *Fagus* and *Castanea* sites (see p. 498). *Adoristes ovatus* was a typically opportunistic species, feeding predominantly on fungi in the autumn and phanerogam material in the summer, while certain individuals of species in three genera of Phthiracaroidea (usually considered to be the macrophytophagous group *par excellence*) contained nothing but fungal material (cf. Hartenstein, 1962*a*, who recorded occasional selection of fungi in phthiracaroid cultures). The use of different culture techniques and foods may also be responsible for some of the conflicting reports in the literature. For example, *Nothrus palustris* is

described by Lebrun (1970 and personal communication) as a typical macrophytophage, feeding on microbially conditioned leaves, preferably of species with a low C:N ratio, such as *Alnus*; Luxton (1972), however, found that this species consumed only small amounts of *Fagus* leaves, but fed readily on a wide range of fungi, and he therefore classified it as panphytophagous.

Because of this variability, rigid categorization of feeding habits of particular microarthropods should be avoided until more data are available, but a selection of examples belonging to the main feeding types is included here.

Out of 14 collembolan species from a mixed woodland, Dunger (1956) found *Lepidocyrtus* spp. and *Entomobrya muscorum* Nicolet to be predominantly mycophagous, the gut contents of the remainder (panphytophagous species of *Tomocerus*, *Orchesella*, *Folsomia* and *Onychiurus*) including at least 50% leaf material. Half of the oribatids described by Schuster (1956) as microphytophagous, such as *Amerus troisii* (Berlese) and *Oppia subpectinata* (Oudemans), seemed to prefer fungi. *Ceratoppia bipilis* and *Belba kingi* were among several oribatid species designated as strictly fungivorous by Hartenstein (1962*a*), the latter species belonging to the superfamily Damaeoidea which, together with the Oppioidea and possibly the Eremaeoidea, Luxton (1972) suggests are wholly microphytophagous groups. *Cepheus latus*, *Hermanniella granulata* and phthiracaroids are classified by Luxton as macrophytophagous, leaving the majority of oribatids, such as species of *Camisia*, *Platynothrus*, *Carabodes*, *Ceratozetes*, *Hermannia*, *Adoristes*, *Liacarus* and *Nothrus*, as panphytophagous.

Hartenstein (1962*a*, 1962*c*) described certain panphytophages, such as *P. peltifer*, as primarily fungivorous while also being able to consume decomposing litter (Fig. 11), and Luxton (1972) has pointed out that this plasticity is of ecological advantage, enabling certain species to exploit a variety of habitats.

The vertical distribution of types of litter or micro-organisms suitable for particular microarthropod species or their immatures may be largely responsible for species distribution patterns in the field (Anderson, 1971; Luxton, 1972). Anderson and Healey (1972), in trying to explain the combination of high species diversity with a comparatively low degree of feeding specificity in detritivore communities, such as Collembola, suggested that interspecific competition is possibly reduced not only by different vertical distributions, but also by the horizontal compartmentalization of resources. Other suggestions included the presence of excess food for decomposers, possibly aided by non-feeding phases associated with moulting, and undetected differences in the digestive abilities of the various species, with further sharing of resources through coprophagy.

III. Microarthropod Energetics

From the point of view of litter breakdown, we need to know the amount of litter which is processed by microarthropods, that is, transformed

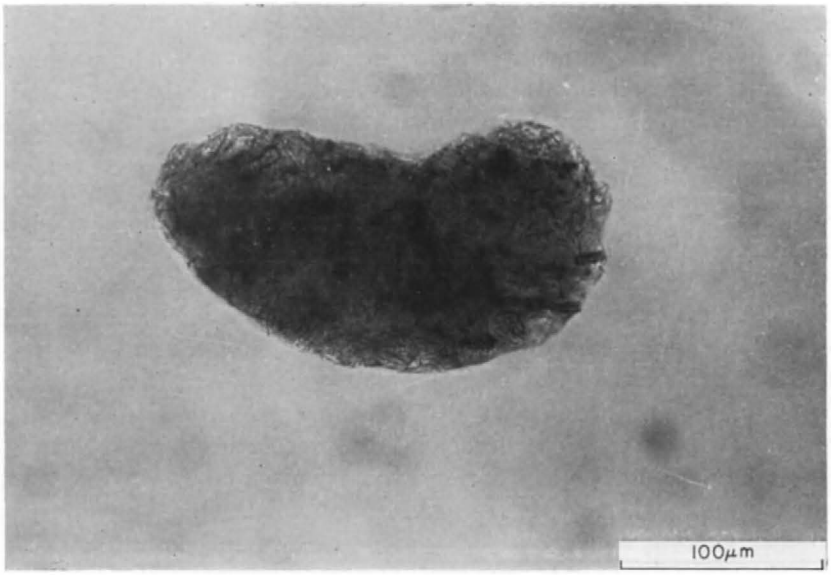


Fig. 11. Faecal pellet produced by *Platynothrus peltifer* adult cultured on decomposing *Quercus* leaf. (Photograph by P. W. Murphy.)

chemically or physically, mainly as a result of being ingested. Some of this food is passed out as faeces, while the remainder is assimilated and metabolized, the associated energy being represented in production (growth, exuviae and reproductive products) and respiration (maintenance metabolism). The energy relationships may be represented by two equations:

$$C = A + FU$$

and

$$A = P + R$$

where C = consumption (ingestion); A = assimilation; FU = rejection (normally considered in microarthropod studies as undigested faecal material); P = production; R = respiration.

These litter feeders effect some chemical decomposition of ingested material as it passes through the gut, but litter decomposition is probably

mainly dependent on the subsequent utilization of their faeces by other organisms, breakdown of their body tissues by predators and decomposers being of indirect significance. We are, therefore, primarily interested in the amounts of litter ingested, assimilated and defaecated by microarthropods. Recently, much information has been published about energy flow in soil ecosystems, but this refers mainly to maintenance metabolism or, occasionally, to production, and generally there are only very approximate estimates of ingestion and defaecation rates for particular populations.

A. Amounts of Litter Processed

Gravimetric determinations of litter consumption by microarthropods are complicated by inaccuracies arising from the small amounts ingested and from estimates of the oven-dry weight of the actual food. Thus, Noordam and Vlieger (1943), Spencer (1951) and Hayes (1963) all recorded instances of controls losing more weight than litter exposed to animals, so that Spencer doubted the validity of his few positive results, one of which is given in Table I.

TABLE I. Ingestion (*C*) and defaecation (*F*) rates of Acari[a]

Taxon	*C*	*F*	Food	°C	Author
Steganacarus magnus	3·5	1·7	*Fraxinus*	4	Spencer (1951)
Steganacarus magnus	—	1·9	*Quercus* (fresh)	20	Madge (1964)
Steganacarus magnus	—	2·5	*Quercus* (old)	20	Madge (1964)
Steganacarus magnus	5·2–5·5	—	*Quercus, Fagus*	18	Berthet (1964)
Steganacarus magnus	8·3–8·7	—	*Corylus, Carpinus*	18	Berthet (1964)
Steganacarus magnus	—	11	*Corylus*	22	Berthet (1964)
S. magnus (young and old ♂♂, ♀♀)	6·3–15·1	3·2–6·3	^{32}P-*Calluna*	18	Webb and Elmes (1972)
Cultroribula juncta	1·06	—	^{45}Ca-*Pinus* mor	20	Kowal (1969)
Oribatids (mean for 7 species)	2	—	*Quercus*	Summer	Witkamp (1960)
Oribatids (mean for 7 species)	0·7	—	*Quercus*	Winter	Witkamp (1960)
Damaeus clavipes (nymphs, adults)	0·4–5·8	0·1–2·2	^{32}P-fungus	15	Luxton (1972)
Nothrus biciliatus	65[b]	—	Yeast	28	Saichuae *et al.* (1972)
Astigmata (4 species)	10[b]–50[b]	—	*Neurospora*	27	Pimentel *et al.* (1960)

[a] μg oven-dry weight ingested or defaecated per mite per day.
[b] μg fresh weight ingested per mite per day.

It should be easier to assess weights of defaecated material, but relevant data are scarce. Gravimetric estimates in Table I refer mainly to *S. magnus*, for which a comparison of rates at 10°C and 20°C (Madge, 1964) indicates a Q_{10} of *ca.* 1·6; we have obtained similar results (unpublished) with *R. duplicata* on *Fagus* leaves.

Radiotracers have been used in attempting to quantify feeding on phanerogams and fungi, but the results need to be interpreted carefully (Reichle and Crossley, 1965; Kowal and Crossley, 1971). Various methods and formulae can be used, but it is usually assumed that both radiotracer and food are assimilated in similar proportions, and that the accumulated material occupies a single body-pool. Engelmann (1961) fed yeast containing ^{14}C-labelled glycine to an unnamed oribatid and estimated that the ingestion rate per day was equivalent to 40% of dry body-weight and the assimilation rate to 8%, giving a value for the assimilation/consumption ratio (as a percentage) of 20%; these values were then applied to an old-field mite population, with an average biomass of 54 mg m^{-2}, to obtain figures of 10,248 cal ingested and 2058 cal assimilated m^{-2} $year^{-1}$.

Using Kowal's (1969) data for the oribatid *Cultroribula juncta*, and assuming an exponential relationship between temperature and ^{45}Ca elimination, Kowal and Crossley (1971) estimated weight-specific ingestion rates for various groups feeding on *Pinus echinata* mor, i.e. forest-floor material (Table II). Their values are lower than some given in Table II, possibly because of the values assigned to the elimination rates; however, when applied to a field population of Collembola and oribatids with a biomass of 200 mg m^{-2}, a rate of 0·046 is equivalent to an ingestion of 9·1 mg m^{-2} day^{-1} or, with approximate temperature corrections, to an annual consumption of 0·5% of the total detritus input of the *Pinus* forest floor. The data in Table II suggest that ingestion rates per day range from 1 to 40% of dry body-weight.

Accurate measurements can be made of the area of food consumed, particularly when leaves are perforated, and these values can be converted to volume or weight. Dunger (1956) gives an average ingestion rate of 0·049 mm^3 day^{-1} at 18°C for *F. fimetaria* on leaves of various trees, while *O. armatus* at similar temperatures was estimated by Witkamp (1960) to consume 0·07 mm^3 day^{-1} of *Mortierella pusilla* mycelium.

Berthet (1964) used planimetry to assess the ingestion of leaf litter by *S. magnus* at 18°C, noting that it was difficult to take partial perforation into account. The ingestion rates quoted in Table I were derived by using the area/weight ratio of the litter, but no allowance was made for differential feeding on vascular and intervein tissues. Defaecation rates were determined at 22°C, the mean dry weight of 1·7 μg per pellet being identical to Madge's (1964) value for this species. Berthet then applied a respiration/

temperature regression to estimate that a mite weighing 360 μg would use 1·5 μl of O_2 per day at 22°C, equivalent to the complete combustion of 1·86 μg of carbohydrate. Adding this value to 11 μg of faeces, he concluded that 12·9 μg of litter had been ingested, giving an A/C ratio of 14%. A similar approach was used by Berthet to calculate the amount of litter which

TABLE II. Weight-specific ingestion rates[a] of microarthropods

Taxon	Ingestion rate	Food	°C	Author
One oribatid species	0·40	^{14}C-yeast	?	Engelmann (1961)
C. juncta	0·25	^{45}Ca-*Pinus* mor	20	Kowal (1969)
Oribatids (adult)	0·125	^{45}Ca-*Pinus* mor	Field (*ca.* 20)	Kowal and Crossley (1971)
Oribatids (immature)	0·059	^{45}Ca-*Pinus* mor	Field (*ca.* 20)	Kowal and Crossley (1971)
Collembola	0·018	^{45}Ca-*Pinus* mor	Field (*ca.* 20)	Kowal and Crossley (1971)
Oribatids and Collembola	0·046	^{45}Ca-*Pinus* mor	Field (*ca.* 20)	Kowal and Crossley (1971)
S. magnus (young and old, ♂♂, ♀♀)	0·03[b]–0·08[b]	^{32}P-*Calluna*	18	Webb and Elmes (1972)
S. magnus	0·02[b]–0·04[b]	*Fagus*, *Corylus*	18	Berthet (1964)
Phthiracaroids	0·01	^{137}Cs-*Liriodendron*	20	McBrayer and Reichle (1971)
Fungivorous microarthropods	0·04	^{137}Cs-*Liriodendron*	20	McBrayer and Reichle (1971)
D. clavipes (nymphs and adults)	0·06–0·09	^{32}P-fungus	15	Luxton (1972)
Onychiurus procampatus	0·25[c]–0·38[c]	Fungi	15	Healey (1967)

[a] μg ingested/μg body weight/day; both weights oven-dry.
Dry body weight assumed to be [b]60% or [c]45% of fresh weight.

would have to be ingested to account for the annual oxygen consumption of the oribatid population of a *Quercus* forest floor (Berthet, 1963). Adult respiration rates for 16 species were measured in the laboratory, Q_{10} values ranging from 2·6–5·6 (average *ca.* 4) for 5–15°C. The relationship between body weight and respiration rate was studied in *S. magnus*, and a common regression of mean body weight on respiration was established for the 16 species. Using this information, the oxygen requirements of each of 46 species were calculated with reference to monthly abundance figures and mean temperatures of the forest floor, yielding an annual adult consumption of 4·5 l O_2 m^{-2}. The formula used to calculate adult respiration rates from body weight and temperature was applied to abundance data

for all developmental stages in a *Pinus* forest, and it was concluded that 70% of the total oribatid respiration rate was accounted for by immatures. The annual total for the *Quercus* population was therefore increased to 10–15 l m^{-2}, corresponding to the combustion of 12–19 g carbohydrate. Taking 10% as a value for A/C in the oribatids, while admitting that the only data available were for *S. magnus*, Berthet estimated that *ca.* 150 g m^{-2}, half the annual leaf-fall, were ingested by oribatids in this site. Berthet (1967) later calculated annual respiration rates for adult oribatids in the litter of a number of woodland sites; these ranged from 33 to 123 ml O_2 l^{-1} of litter. Allowing for the activities of immatures and humus dwellers, he obtained an average value for energy flow of 30 kcal m^{-2} for forest oribatids, which, with an A/C value of 14%, gave an annual ingestion equivalent to *ca.* 20% of the annual litter fall.

Despite the uncertainties inherent in extrapolating from laboratory determinations to natural populations (Macfadyen, 1967; Berthet, 1971), Berthet's respiration data are the most comprehensive so far, since they include specific, seasonal fluctuations, as well as indicating the relative significance of various species in terms of annual oxygen consumption. Berthet (1967) stressed that in each site at least half of the total respiratory activity was accounted for by only four species, usually large mites such as *S. magnus*, *P. peltifer* and *N. palustris*, but with *T. velatus* compensating for small size by great abundance in a coniferous site.

However, Berthet's estimates of assimilation and ingestion rates may have to be reconsidered in the light of more recent results. Berthet (1964) quoted Engelmann's (1961) value of 20% for the A/C ratio to support his suggestion that this ratio might be higher in mycophages than the range of 5–14% for macrophytophages such as *S. magnus*, diplopods and isopods. Considerably higher values have in fact been obtained for mycophages by Healey (1967) and Luxton (1972). Healey gives values of 40–70% for *O. procampatus*, depending on fungal species, while Luxton's values for *D. clavipes*, based on ^{32}P uptake, range from 47% in tritonymphs to *ca.* 62% for the other nymphal stages and adults. Luxton pointed out that the use of phosphate possibly gives a false picture of general food requirements, especially in immatures, but nevertheless he suggested that A/C ratios for microphytophages in general might be 50–65%. High values were possibly achieved with *D. clavipes* protonymphs and adults by slow movement of relatively rich food through the gut, defaecation rates of *ca.* 0·75 pellets per mite per day being contrasted with a mean of 6·5 for *S. magnus* on *Corylus* (Berthet, 1964). Luxton tentatively suggested A/C ratios of 40–50% for panphytophages and 10–15% for macrophytophages. However, Webb and Elmes (1972), also using ^{32}P, calculated that young adults of *S. magnus* assimilated 58% of ingested *Calluna* litter, the ratio falling to 52% and

19% in mature females and males, respectively; when calculated in terms of calorific values of food and faeces, values ranged from 41 to 69%. Ingestion rates were comparable to those given by Berthet (1964; see Table I) and although defaecation rates were about half those quoted by Berthet for *Corylus* (Table I), they were about twice the rates for *Quercus* (Madge, 1964). Since defaecation was assessed gravimetrically by Webb and Elmes, major errors seem more likely to have arisen from non-uniform distribution of ^{32}P in the food, thus leading to inaccurate estimates of ingestion. Nevertheless, these results indicate the need for more studies before we can make valid generalizations about assimilation/consumption ratios.

Berthet (1967) assumed that only a small part of the energy assimilated by soil organisms is used for biosynthesis, and in fact his conversions of oxygen consumption to ingestion rates make no allowance for production. Admittedly, Engelmann (1961) had estimated that 95% of the energy assimilated by an old-field mite population was respired, and Macfadyen (1969*a*) considered this to be a realistic value in sluggish mites which presumably feed on relatively non-nutritious foods. However, both Berthet (1964) and Macfadyen (1969*a*) realized that Engelmann's numerical values were unreliable in several respects; for example, estimates of production were based on rather atypical generation times for one species. Webb and Elmes (1972) calculated the amount of energy available for production in *S. magnus* by finding the difference between assimilation and respiration, when feeding on *Calluna*, and obtained P/A percentages of 96, 74, and 88 for young adults, mature females and males, respectively. Respiration rates were similar to those given by Berthet (1964), and these high values for production may be based on inaccurate ingestion and assimilation data. Webb and Elmes, however, consider that their estimates of production could be accounted for by cuticular thickening in young adults, and reproduction in mature adults. Thomas (1972) gives a P/A percentage of *ca.* 27, and an A/C percentage of *ca.* 32, with an annual ingestion of *ca.* 18 kcal m^{-2}, for the oribatid population of the I.B.P. deciduous woodland site at Meathop.

Michael (1884) commented on the special vigour of immature oribatids' feeding, but there have been very few quantitative assessments of this vigour. Saichuae *et al.* (1972) recorded similar ingestion rates for tritonymphs and adults of *N. biciliatus* on yeast, whereas Luxton (1972) found that adults of *D. clavipes* ingested *ca.* 4, 8 and 15 times as much fungus as tritonymphs, deutonymphs and protonymphs, respectively. Luxton's figures have not yet been applied to field populations, as Webb (1970*a*) did for respiration rates of the various stages of *N. silvestris*. Laboratory estimates of these rates (Webb, 1969; see Table III) were applied to a heathland population, with temperature corrections as determined for

adults, and it was calculated that immatures contributed 61 ml and breeding adults 28 ml to an annual total of 119 ml O_2 m^{-2}; tritonymphs were responsible for 27% of this total, deutonymphs for 13%, protonymphs for 7% and larvae for 5%. In July, breeding adults represented 40% of the population, but accounted for 80% of the total metabolism.

Thomas (1972) has found that dry-weight-specific respiration rates of adults and tritonymphs have comparable values in species such as *P.*

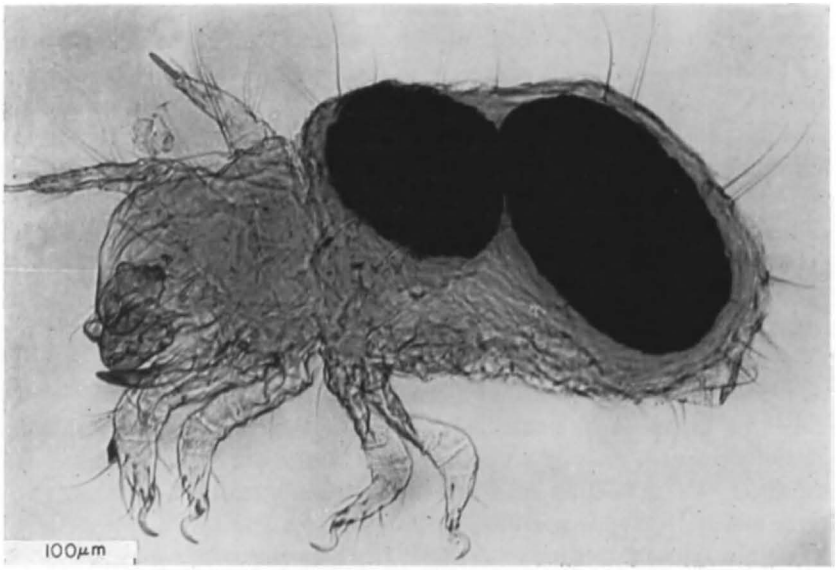


Fig. 12. Tritonymph of *Rhysotritia duplicata*, containing two food boluses. (Photograph by P. W. Murphy.)

peltifer, *N. silvestris* and *H. gibba*, being approximately half the corresponding values for protonymphs and deutonymphs. Harding (1966) recorded the production of up to ten faecal pellets per day at 15°C by individual tritonymphs (Fig. 12) and adults of *R. duplicata*. These pellets were of similar dimensions in the two stages, whereas in *P. peltifer*, where rates of up to 15 per day by nymphs were somewhat higher than in adults, pellet breadths decreased in the ratio 17:11:9:7:4 between the adults, three nymphal stages and larvae (see also Saichuae *et al.*, 1972); the volume of an adult pellet is *ca.* 100× that of a larval pellet. Even with a maximum abundance ratio of 18 larvae to 1 adult in a *Pteridium* site (Harding, 1973), the volume of litter processed by immatures of this species may therefore be less than by adults, especially when culture studies suggest that 35–86% of the duration of each immature stage may be spent in preparing to moult and in ecdysis (Jalil, 1963), so that 17% of all immature

individuals (29% of larvae) in a field population had no gut contents (Harding, 1966). The situation may be reversed, however, in those oribatid species in which the adults apparently feed only for a small fraction of their life-span (Woodring, 1963). More data are required on the relative importance of adults and immatures of a range of species, in terms of ingestion, assimilation and respiration.

B. Other Aspects of Microarthropod Populations

There are many published estimates of collembolan density, habitats ranging from deserts to arctic/alpine and tropical woodland. A comparison of extraction methods for terrestrial arthropods has been made by Edwards and Fletcher (1971). Mean densities (in thousands per m^2) range from 0·11 for desert (Wallwork, 1972) to 109 for temperate permanent grassland (Haarløv, 1960). Maximum densities may rise to over $200 \times 10^3\ m^{-2}$ in permanent pasture and antarctic moss- and lichen-covered formations (McMillan, 1969; Tilbrook, 1970). It is noteworthy that figures for tropical woodland are towards the lower end of the range of densities (Block, 1970; Greenslade and Greenslade, 1968; Drift, 1963).

Published estimates of mean density figures for oribatid mite populations range from 6·7 to $134 \times 10^3\ m^{-2}$ (Berthet, 1963, 1967; Block, 1966; Harding, 1966).

Estimates of biomass are fewer and they may be affected by the assumptions made in order to arrive at them. These include the use of adult mean weight and the assumption that all the individuals encountered are adults. Published figures give a range for annual mean biomass (mg live wt m^{-2}) for Collembola from about 30 (Dunger, 1968) to 3160 (Lebrun, 1971). For oribatids, the range is from 300 to 5400 (Berthet, 1963, 1967; Block, 1966; Harding, 1966; Thomas, 1972). These biomasses are low in comparison with those of earthworms, enchytraeids and nematodes.

Estimates of annual mean respiration rates for microarthropod populations are beset with the same difficulties as estimates of annual mean biomass with the additional problems of extrapolating from laboratory determinations to field conditions and making suitable corrections for fluctuating physical conditions encountered in the field (cf. Phillipson, 1963; Macfadyen, 1967).

Weight-specific respiration rates are shown in Table III for a range of microarthropods. One obvious feature is the variability between species but with an underlying trend of a decrease in weight-specific rate with increasing weight.

It has been considered that the comparison between the metabolic activity of different populations, rather than a comparison between their

density or biomass, may be a good way of assessing the impact of an animal on its environment (Berthet, 1971). Annual mean respiration rates for Collembola populations appear to lie within the range of 1 to 46 kcal m^{-2} $year^{-1}$ (Bornebusch, 1930, recalculated by Macfadyen, 1963; Cragg, 1961; Drift, 1951; Dunger, 1968; Hale, 1966; Healey, 1967). Annual rates for oribatid populations may reach 30 kcal m^{-2} $year^{-1}$ (Berthet, 1967).

These respiration rates are, however, much lower than those quoted for some other edaphic animal groups, e.g. nematodes in grassland 150–350 kcal m^{-2} $year^{-1}$ (Nielsen, 1949) and earthworms 110 kcal m^{-2} $year^{-1}$ (Satchell, 1967).

In recent years a number of generalized relationships have been determined which possess important predictive possibilities for the study of the energetics of microarthropod populations (Edwards, 1967; Berthet, 1971).

TABLE III. Weight-specific respiration rates of oribatids, Collembola and mesostigmatids

	Taxon	Weight (μg)	Respiration ($\mu l\ g^{-1}\ h^{-1}$)	Author key
Oribatids[a] at 15°C	*Oppia nova*	1·7	380	B
	O. subpectinata	3·2	417	B
	Nothrus silvestris, larva	3·5	259	W
	Tectocepheus velatus	4·2	215	B
	Hypochthonius rufulus	4·4	1980	B
	Chamobates cuspidatus	6·5	728	B
	N. silvestris, protonymph	6·8	351	W
	N. silvestris, deutonymph	12·9	281	W
	Nanhermannia elegantula	18·1	181	B
	N. silvestris, tritonymph	30	261	W
	Oribatella quadricornuta	38	200	B
	Parachipteria willmanni	40	311	B
	Carabodes marginatus	40	95	B
	N. silvestris, adult	52	197	W
	N. silvestris, gravid	53	312	W
	Rhysotritia ardua	57	130	B
	Platynothrus peltifer	63	198	B
	Liacarus coracinus	90	288	B
	Steganacarus magnus ♂	109	72–108	W & E
	S. magnus	249	96	B
	S. magnus, young ♀	291	52	W & E
	S. magnus, mature ♀	436	103	W & E

Table III—*continued*

	Taxon	Weight (μg)	Respiration (μl g^{-1} h^{-1})	Author key
Collembola[b] at 15°C	*Folsomia quadrioculata*	3	1830	S
	Isotoma notabilis	3	2470	S
	Onychiurus procampatus	10	1000	H
	I. notabilis	15	1345	S
	F. quadrioculata	30	615	S
	O. procampatus	50	460	H
	O. procampatus	100	320	H
	O. armatus	132	515	Z
	I. viridis	718	446	Z
Mesostigmatids[c] at 15°C	*Rhodacarus roseus*	7·9	1525	
	Eviphis ostrinus	28	729	
	Cilliba cassidea	45	297	
	Holoparasitus inornatus	66	464	
	Pachylaelaps lindrothi	82	369	
	Geholaspis longispinosus	169	397	
	Pergamasus sp.	582	278	

[a] Calculated from B Berthet, 1963.
W Webb, 1969.
W & E Webb and Elmes (1972).

[b] Calculated from S Stuttard, 1972.
H Healey, 1967.
Z Zinkler, 1966.

[c] Calculated from Webb, 1970*b*.

Probably the most extensive are those of McNeill and Lawton (1970) and Reichle (1971). McNeill and Lawton extended the work of Engelmann (1966) and produced the following relationships for comparatively short-lived poikilotherms (populations in which all the individuals are less than two years of age, i.e. applicable to microarthropods)

$$\log_{10} R = 1{\cdot}740 \log_{10} P + 0{\cdot}1352$$

and

$$\log_{10} P = 0{\cdot}8262 \log_{10} R - 0{\cdot}0948$$

where R is the annual population respiration and P is the annual population production, each expressed as kcal m^{-2} year. Reichle (1971) developed a

relationship between ingestion and biomass of the form

$$\log_{10} \text{calories ingested per day} = \log_{10} 0{\cdot}071 + 0{\cdot}725 \log_{10} \text{calories per individual}$$

He thus showed that energy intake closely follows the body surface/volume relationship for food intake ($b = 0{\cdot}67$) first postulated by Drift (1951). Reichle provided, in addition, a general relationship between body size and metabolic rate for decomposer organisms, of the form

$$\log_{10} \text{metabolic rate } (\mu l\ O_2\ h^{-1}) = \log_{10} 0{\cdot}339 + 0{\cdot}808 \log_{10} \text{live weight (mg)}$$

The use of relationships such as these should allow first approximations to be produced for whole ecosystems in advance of more detailed, but time-consuming, work.

IV. Significance of Microarthropods in Litter Decomposition

A. Chemical Changes

Microscopic examination of gut contents and faeces of litter-feeding microarthropods, with selective staining for cellulose and lignin, led Dunger (1956), Schuster (1956) and Poole (1959) to conclude that vascular and epidermal tissues were practically unaffected, and that digestion was virtually restricted to mesophyll tissues. Drift (1965) suggested that proteins and soluble carbohydrates could provide some sustenance for litter ingesters, but Engelmann (1961) and Burges (1965) indicated that the quantities remaining are usually likely to be small, because of microbial action and leaching, both before and after leaf-fall, and through translocation. Since mites and Collembola are normally thought to resemble other members of the mesofauna in lacking enzymes to digest celluloses, hemicelluloses or lignins (Nielsen, 1962), it is often assumed that litter-feeders are dependent on micro-organisms possessing the requisite enzymes or colonizing freshly fallen litter, either microbial protoplasm, or exometabolites, or both, being digested (Murphy, 1953; Engelmann, 1961). Hyphal fragments may not undergo much evident, structural change in the oribatid gut (Dudich *et al.*, 1952), but Schuster (1956) frequently observed that mycelial contents had disappeared between ventriculus and rectum. Alternatively, Collembola might digest lipids and carbohydrates selectively, without affecting fungal viability (Healey, 1967).

Whole-body homogenates of species of *Phthiracarus*, *Eupelops* and *Nothrus* (representing the main oribatid feeding-types) and of *Tomocerus* and *Onychiurus* were shown by Zinkler (1971) to possess trehalase activity,

which Luxton (1972) failed to demonstrate in two *Steganacarus* species or in some of his panphytophagous species, although trehalase, and possible chitinase, were detected in microphytophages. Zinkler concluded that Collembola and microphytophagous oribatids differed from panphytophages and macrophytophages in being unable to utilize structural polysaccharides such as carboxymethyl cellulose, xylan and pectin, hydrolytic activity being confined to microbial intracellular components. On the other hand Luxton suggested that whereas microphytophages might be able to attack hyphal walls, macrophytophages, apparently lacking chitinase and trehalase, would be unable to digest much fungal material, and might actually compete with cellulolytic micro-organisms, since he, unlike Zinkler, detected cellulase activity in phthiracaroid homogenates. Among earlier references to cellulases in oribatids, Kühnelt (1961) claimed, without any supporting details, that scarcely any cellulose residues remain in litter after passing through oribatids, while Gasdorf and Goodnight (1963) recorded decreases in the cellulose content of *Quercus* leaves after processing by either *Hermanniella* sp. or *Peloribates* sp.

However, even if cellulolytic activity is demonstrated in homogenates, this does not necessarily prove that the species concerned can utilize cellulose as it occurs in plant tissues (Nielsen, 1962), even though mastication may help to uncover cellulose and also lignin (Dunger, 1956). More sophisticated analytical techniques are needed to ascertain the enzymatic potential of microarthropods and their gut flora, but there are already indications that their role as primary decomposers may be greater than was previously believed.

B. Physical Changes

In contrast to chemical decomposition, the physical effects of microarthropod feeding are usually obvious. Litter and hyphae are comminuted by the mouthparts into fragments ranging in size from a few microns to more than 100 μm. Vascular-bundle fragments 150 $\times$ 30 μm have been observed in collembolan faeces (Dunger, 1956), while fragments of *Quercus* leaf may be 100 μm across in *Nothrus* pellets (Bal, 1968), and pieces of hypha up to 120 μm long are common in oribatids and Collembola (Harding, 1966; Anderson and Healey, 1972). There is some evidence that smaller species of oribatids effect a finer comminution than large ones (Tarman, 1968), and the same is probably true of immature microarthropods. Average fragment sizes recorded include 5 $\times$ 3 μm for *S. magnus* (Spencer, 1951), and 20 $\times$ 12 μm for *N. silvestris* (Bal, 1968), while McMillan and Healey (1971) found that 27–93% of plant fragments in seven collembolan species were $<$10 μm across.

These fragments leave the body as faeces, ranging in form from droplets and crumbs in microbivorous Collembola (Zachariae, 1963) to pellets of definite shape, such as spherical, kidney-shaped or ovoid (common in oribatids) and cylindrical, which are possibly more characteristic of certain Collembola. Both form the size of pellets can vary in the same individual, e.g. with type of food (Drift, 1965; Harding, 1966), but published sizes range from 12 × 17 μm in *R. minima* immatures (Bal, 1968) and 20 μm diameter droplets in certain Collembola (Zachariae, 1963), via 175 × 95 μm in *N. biciliatus* (Saichuae *et al.*, 1972) to 220 × 120 μm in *P. peltifer* (Harding, 1966) and 240 × 140 μm in *O. armatus* (Witkamp, 1960).

C. Effects on Other Organisms

Mastication exposes resistant compounds which then become concentrated in pellets, forming foci of high nutrient status (Macfadyen, 1961) which are potentially usable by micro-organisms and coprophages. The greater surface area resulting from comminution increases the accessibility of substrates, especially to bacteria (Engelmann, 1961). Nef (1957) calculated that the conversion of a 60 mm conifer needle into 10 μm^3 fragments by phthiracaroids results in an increase of 10^4 times in surface area, although the pellets' surface area represents only a fourfold increase. Even pellets, however, move down the organic profile to regions of greater microbial activity more rapidly than does the intact litter (Witkamp, 1971).

Microbial accessibility to tissues around feeding cavities may be facilitated by the clearing away of material during ingestion (Engelmann, 1961), and decomposition may also be accelerated by microarthropods browsing on mature and senescent microbial colonies (Macfadyen, 1961, 1964). McBrayer and Reichle (1971) estimated that 60% of the soil-invertebrate biomass in a *Liriodendron* site was represented by fungivores, ingesting an average of 7% of their body weight per day.

The various ways in which microarthropods may influence microorganisms are discussed by Kühnelt (1963). The limited mobility of many elements of the microflora (Macfadyen, 1964) may be overcome by dissemination via animals, perchance to environments which are more favourable in terms of climate, food and biostasis. Dispersal of fungal spores on the surface of microarthropods was demonstrated by Jacot (1930) and Witkamp (1960), while viable microbial material has been recovered from faeces by Poole (1959), Witkamp (1960) and Mignolet (1971). Kühnelt (1961) and Healey (1970) found that hyphae and undamaged spores germinated freely after passing through Collembola, whereas Drift (1965) and Cervek (1971) recorded drastic reductions in viability. Zachariae (1963) suggested that other agents, such as wind and

rain, are more important in dispersing micro-organisms, but dispersal and comminution are probably the major contributions of microarthropods to litter decomposition (Healey, 1970; Kevan, 1962).

D. Decomposition Rates

The statement by Burges (1965) that litter decomposition is retarded after the initial, microbiological phase, and might even stop were it not for faunal activity, was based largely on studies of *Pinus*-needle decomposition in a mor site with a significant population of microarthropods (see p. 498). Exclusion experiments using naphthalene (Kurcheva, 1960; Crossley and Witkamp, 1964) indicated that tree leaf-litter lost weight more rapidly when animals were present, microarthropods being the most adversely affected group in Crossley and Witkamp's treated plots. Somewhat equivocal results have been obtained by excluding certain sizes of animal from litter in mesh bags. Edwards and Heath (1963) and Anderson (1970) found that microarthropods were relatively unimportant in the disappearance of *Quercus* or *Fagus* litter in woodland sites with high densities of lumbricids or diplopods. Weight losses recorded by Anderson from *Castanea* litter in bags with meshes of 7 mm, 1 mm and 48 μm indicated that soil animals in that site had little effect on the breakdown of primary leaf structure, being mainly mycophagous and detritus feeding, whereas abiotic leaching had a marked influence. Heath *et al.* (1966), Curry (1969*a*) and Zlotin (1971) found that animals had little or no effect on disappearance rates of *Lactuca sativa* (lettuce) and grasses from mesh bags. However, Madge (1965) found a clear correlation between the abundance of microarthropods and the area of tree leaf-litter lost from bags in a Nigerian forest site where lumbricids and macroarthropods were unimportant, and Zlotin (1971) recorded a doubling of the rate of disappearance of *Quercus* leaves from bags to which the mesofauna had access, compared with purely microbial attack. Finally, the role of Collembola in the breakdown of *Quercus* litter was demonstrated by Edwards (1965), their populations being artificially increased by applications of DDT to the soil.

Careful consideration should be given to litter-bag techniques and results, since exclusion may not be perfect and weight loss is not solely due to decomposition. However, it appears that in certain sites microarthropods are not important, at least during the initial breakdown of litter.

In the coprogenous part of the humus, on the other hand, one would expect to find evidence of increased decomposition rates (Kubiena, 1964). Zachariae (1965) observed that pellets of litter-ingesting mites and Collembola were readily colonized by micro-organisms and ingested by

lumbricids, but the faeces of microbivorous Collembola were scarcely attacked at all, and contributed to the amorphous humus (see also Jongerius, 1963). Grossbard (1969) recorded rapid distintegration of ^{14}C-labelled grasses, but faecal pellets, which were assumed to contain the more indigestible constituents, remained intact at the soil surface for more than a year. The relative persistence of pellets has been recorded for certain oribatids, particularly phthiracaroids; Schuster (1956) found pellets which had been in a tree stump for over a year, while Bal (1968) recorded that phthiracaroid pellets retained their identity even after ingestion by lumbricids. The stability of oribatid pellets may be partially due to a peritrophic membrane (Harding, 1966, 1967; Bal, 1968) (Fig. 9).

The disintegration of pellets, described in detail by Bal (1968), presumably leads to greater decomposition rates, due to microbial action and leaching, but comparative data for these rates and those of remains which have only been leached and microbially attacked are scarce. Anderson (1970) suggested that fragmentation increased decomposition rates in his *Fagus* site, but apparently had no effect in the *Castanea* site.

V. Conclusions

Large numbers of microarthropods are dependent on decomposing plant material, but it is difficult to assess the extent to which decomposition is dependent on microarthropods. Their influence would seem likely to be greatest in pioneer soils and in mor and certain moder sites (Kubiena, 1953, 1955; Haarløv, 1960; Jacks, 1965; Nosek, 1967; Hale, 1967), where, as Wallwork (1967) has pointed out, the long-term effects of animals with a low population metabolism may be of greater significance than the spasmodic influence of a relatively scarce macrofauna. In terms of maintenance metabolism and chemical decomposition of litter, microarthropods are of minor importance compared with the microflora. Interpretations of soil sections often indicate the dominant role of the macrofauna in determining profile characteristics (Zachariae, 1963, 1965), but a combination of gut-content analysis with micromorphological studies of various profiles, as developed by Anderson and Healey (1970, 1972), could yield valuable information on the relative roles of particular groups.

As Drift (1970) has stressed, exact knowledge of feeding habits exists for only a few species of soil animals. The diet of many Prostigmata and of those Collembola with piercing mouthparts, for example, is virtually unknown. In order to assess the role of microarthropods in litter decomposition, more data are needed, from a range of sites, on food selection, litter processing and pellet breakdown, as well as on catalytic interrelations with micro-organisms.

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